

DID A MEMBER OF THE *VANESSA INDICA* COMPLEX (NYMPHALIDAE) FORMERLY OCCUR IN NORTH AMERICA?

RICHARD I. VANE-WRIGHT

Scientific Associate, Dept. of Entomology, the Natural History Museum, Cromwell Road, London SW7 5BD, UK; Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, CT2 7NR, UK; and UK National Endowment for Science, Technology and the Arts; email: dickvanewright@binternet.com

AND

HAROLD W.D. HUGHES

16 Wingfield Road, Kingston-upon-Thames, Surrey KT2 5LR, UK

ABSTRACT. The North American Oligocene fossil *Vanessa amerindica* is thought to be most like *V. indica*. Based on an 18th century painting made by the English naturalist Henry Seymer Jr., the possible existence of a member of the *indica* complex that occurred in North America as late as circa 1770 is demonstrated. New information on the classification of the nine extant species currently included in *Vanessa sensu stricto* strongly suggests that this apparently undescribed species is most closely related to the Atlantic Islands endemic, *V. vulcania*. Three competing scenarios that attempt to explain the highly disjunct distribution of the species that make up the *V. indica* complex are discussed, and it is concluded that the genus *Vanessa* most probably originated in North America, and that *V. vulcania* represents a separate, Atlantic colonisation event, separate from the Pacific colonisation event that gave rise to the Asiatic *V. indica*-group. This implies that, contrary to earlier hypotheses that sought to explain the distributional gap between the Canaries and India, the *indica* complex may never have been established on the western Palaearctic mainland, or in the Eremic Zone (Morocco to Somalia and Tien Shan). An African species formerly placed in *Antanartia* is formally transferred to the genus *Vanessa* (*Vanessa abyssinica*, **comb. nov.**).

Additional key words: Tertiary, relict, introduction, biogeography, Newfoundland, Macaronesia, Henry Seymer.

According to Art Shapiro (1992a), “The most peculiar Palearctic butterfly distribution is that of the Indian Red Admiral, *Vanessa indica* (Herbst).” Although the taxonomy of this member of the Nymphalidae has since changed — *V. indica* (Herbst, 1794), in Shapiro’s sense, is now divided into three allopatric species — the enigma to which he referred remains: how can the 7000 km gap in distribution between the Indian red admirals found on Madeira and the Canary Islands, and those occupying the rest of the range, in the Oriental region and far eastern Palaearctic, be explained? No extant member of the species complex to which these butterflies belong is known from the rest of the western Palaearctic, North Africa, or North America.

Fresh interest in this problem has come from the recent discovery of an 18th century painting of a member of the *Vanessa indica* complex, supposedly based on a specimen collected in Newfoundland circa 1770. This illustration is one of some 300 surviving images of exotic butterflies and moths made by the little-known British naturalist Henry Seymer (1714–1785), together with his son, Henry Seymer Jr. The Seymers obtained their natural history specimens, notably of molluscs and insects, through dealers, travellers, military personnel and other contacts. Based on an extensive analysis of all the known Seymer

Lepidoptera paintings, and their notes and records, it has been demonstrated that the vast bulk of their exotic material came from China, Java, India, West Africa, South Africa, South America, Jamaica, and the early British colonies in North America (Vane-Wright & Hughes, 2005: table 1, p. 254). Their Lepidoptera collection apparently totalled some 20,000 specimens, but it was dispersed immediately after Henry Sr.’s death, and nothing is yet known to have survived (Vane-Wright & Hughes, 2005; Barker & Vane-Wright, 2007).

The Seymer paintings, made during the period 1755–1783, appear to have been intended as a virtual record of the collection. If so, it is fortunate they had such foresight. The level of accuracy achieved ranges from good to outstanding. Minute detail is often finely rendered, and the coloring remains authentic in all but a few instances (Vane-Wright & Hughes, 2005). The lack of degradation of tint that might be expected in such old watercolors is no doubt a consequence of the fact that, through the intervening years, the pictures were rarely on show, and were evidently preserved in library conditions.

The idea that a member of the *V. indica* complex recently occurred in North America is so surprising that, without a specimen and independent verification, considerable doubt must be accepted—although we

believe the case for authenticity (presented below) is good. However, *whatever the final conclusion regarding the painting*, it has stimulated us to review the “*Vanessa indica* problem” and, in turn, challenge two previous hypotheses regarding the biogeography of these butterflies, and support instead an alternative hypothesis in which North America plays a key role.

Phylogenetic Relationships of the Red Admiral Butterflies

The type species of *Vanessa* Fabricius, 1807, *Papilio atalanta* Linnaeus, 1758, is the familiar Red Admiral butterfly. In his major revision, Field (1971) placed five species of red admirals in the genus: *V. atalanta* (L., 1758), *V. tameamea* Eschscholtz, 1821, *V. indica* (Herbst, 1794), *V. dejeanii* Godart, 1824, and *V. samani* (Hagen, 1895), but more species are now recognized (see below). The two other main species groups usually included within the genus are the painted ladies (placed by Field in the genus *Cynthia*; type species *Papilio cardui*) and the antipodal admirals (placed by Field in *Bassaris*; type species *Papilio itea*).

DNA sequence data (Wahlberg *et al.*, 2005) suggest that within *Vanessa* and contrary to earlier phylogenetic work based solely on morphology (e.g. Craw, 1989, Holloway & Nielsen, 1999), the red admirals (*Vanessa sensu stricto*) have a sister-group relationship with *Vanessa abyssinica* (Felder & Felder, 1867), a montane butterfly from East Africa. Previously *V. abyssinica* was treated as a member of the endemic Afrotropical genus

Antanartia Rothschild & Jordan, 1903 (e.g. Howarth, 1966; Ackery *et al.*, 1995).

Superficial comparison indicates that this new arrangement is credible: all five remaining *Antanartia*, including the type species, *Papilio delius* Drury, 1782, have distinct hindwing tails at vein M3, whereas *V. abyssinica* does not, looking instead rather like a small and drab red admiral (Fig. 1a). The work of Nakanishi (1989) on the early stages of *abyssinica* is consistent with this placement, as it has a peculiar setal arrangement in the first larval instar otherwise known only from *Vanessa*, and it shares the habit, in later instars, of making a nest by tying both edges of a leaf together with silk. Nakanishi recorded that neither *Antanartia schaenia* nor *A. hippomene* exhibit these *Vanessa* characters.

However, as also pointed out to us by Thomas Dimock, adult *abyssinica* are highly distinctive compared with all other *Vanessa s.s.* Notably, at least two of the hindwing ocelli always have blue pupils (invariably black in other *Vanessa s.s.*); the hindwing marginal band widens at cell M₁, lacks any black submarginal spots (as seen in an aberration of *V. atalanta*: Frohawk, 1938: p. 86), and continues anteriorly into cell R₅ (unlike other *Vanessa s.s.*); and hindwing vein Sc+R₁ is relatively elongate, giving the wing a unique, almost square aspect. All of these differences can be seen as autapomorphies, except the first, which may be a symplesiomorphy (e.g. this condition is frequent in subgenus *Cynthia*, in *V. (C.) cardui*, for example, being referred to as form

Fig. 1. (on facing page) The species of the genus *Vanessa sensu stricto*. Left halves show upperside, right halves corresponding underside. All figures (with exception of **b**) have been brought to the same forewing length to facilitate comparison; information on actual size is included with each separate legend. With the exception of **b** and **h**, all images are based on specimens in the Natural History Museum, London (BMNH); fw-l. = forewing length. **a**, *V. (Vanessa) abyssinica abyssinica* (Felder & Felder, 1867), male [Ethiopia: Mt Zuqula, over 9000 ft, 25–27.x.1926, H. Scott; BM1927-127; fw-l. 21 mm.] [Howarth, 1966: 31, indicates a range of 17–22 mm for male *V. abyssinica*, and 20–24 mm for female]; **b**, *V. (Vanessa) sp. nov. (V. vulcania-group)*, female? [Newfoundland, ca 1770; from ‘profile’ image made by Henry Seymer Jr., ca 1773; Vane-Wright & Hughes, 2005: 164/5; fw-l. estimated at 35 mm — see text]; **c**, *V. (Vanessa) vulcania* Godart, 1819, female [Spain: Canary [Islands], iv.1855; Leech Collection, BM1901-173; fw-l. 34 mm] [Field, 1971: 24, gives male 26–32 mm, female 29–33 mm, but there are larger and smaller examples in the BMNH collection — see text]; **d**, *V. (Vanessa) indica indica* (Herbst, 1794), male [China: Siao-Lou, 1900; Oberthür Collection, BM1927-3; fw-l. 33 mm] [Field, 1971: 21, gives male 25–34 mm, female 27–37 mm]; **e**, *V. (Vanessa) indica pholoe* (Fruhstorfer, 1912), male [SW India: Anamully Hills, 3000–4000 ft., Davison; Godman-Salvin Collection, BM1903-4; fw-l. 30 mm] [Field, 1971: 22, gives male 27–29 mm, female 28–30 mm]; **f**, *V. (Vanessa) indica nubicola* (Fruhstorfer, 1898), male [Sri Lanka: Newara Eliya, vi.1921, W. Ormiston; BM1922-315; fw-l. 27 mm] [Field, 1971: 22, gives male 26–31 mm, female 30–33 mm]; **g**, *V. (Vanessa) buana* Fruhstorfer, 1898, male [Indonesia: S Sulawesi, Bonthain, 5–7000 ft., x.1895, A. Everett; Rothschild Bequest, BM1939-1; fw-l. 24 mm] [Field, 1971: 23, gives male 27.5 mm; assuming figures in Tsukada, 1985: 82, are life-size, females are ca 25–27 mm]; **h**, *V. (Vanessa) dilecta* Hanafusa, 1992, male [Indonesia: W Timor, Mt Mutis, v.1992; Hanafusa Collection] [Hanafusa, 1992, gives male fw-l. 27.5–30.5 mm, female 30–31 mm.]; **i**, *V. (Vanessa) samani* (Hagen, 1895), male [Indonesia: SW Sumatra, Danau Bento Morass, Ft. of Korintji Peak, 5000 ft., viii.1921, C.F. & J. Pratt, 7.22; Joicey Bequest, BM1934-120; fw-l. 23 mm] [Field, 1971: 27, gives male 25 mm, female 23 mm]; **j**, *V. (Vanessa) dejeanii dejeanii* Godart, 1824, male [Indonesia: E Java, H. Fruhstorfer; Fruhstorfer Collection, BM1937-285; fw-l. 24 mm] [Field, 1971: 26, gives male 23–26 mm, female 23–27 mm]; **k**, *V. (Vanessa) dejeanii sambaluna* (Fruhstorfer, 1898), male [Indonesia: Lombok, Sambalun, 4000 ft., 1896, H. Fruhstorfer; Oberthür Collection, BM1927-3; fw-l. 25 mm] [Field, 1971: 26, gives same size as *d. dejeanii*, including *sambaluna* as a subjective synonym]; **l**, *V. (Vanessa) dejeanii mounseyi* (Talbot, 1936), male [Philippines: [Mindanao]; W. Dannatt Collection, BM1940-130; fw-l. 24 mm] [Field, 1971: 27, gives a value of 26 mm for a male]; **m**, *V. (Vanessa) atalanta atalanta* (Linnaeus, 1758), male [Germany: Berlin: Leech Collection, BM1901-173; fw-l. 30 mm] [Field, 1971: 14, gives male 27–31.5 mm, female 27–34 mm]; **n**, *V. (Vanessa) atalanta rubria* (Fruhstorfer, 1909), male [Canada: Newfoundland, W.C. St. John, 39.9.26. 65 655TM; fw-l. 29 mm] [Field, 1971: 16, gives male 25–34 mm, female 25–35 mm]; **o**, *V. (Vanessa) tameamea* Eschscholtz, 1821, female [USA: Hawaii, Kauai, Mt Waimea, 3000 ft., vi.1894, Perkins; BM1899-227; fw-l. 34 mm] [Field, 1971: 18/19, gives male 31–37, female 32–40 mm].

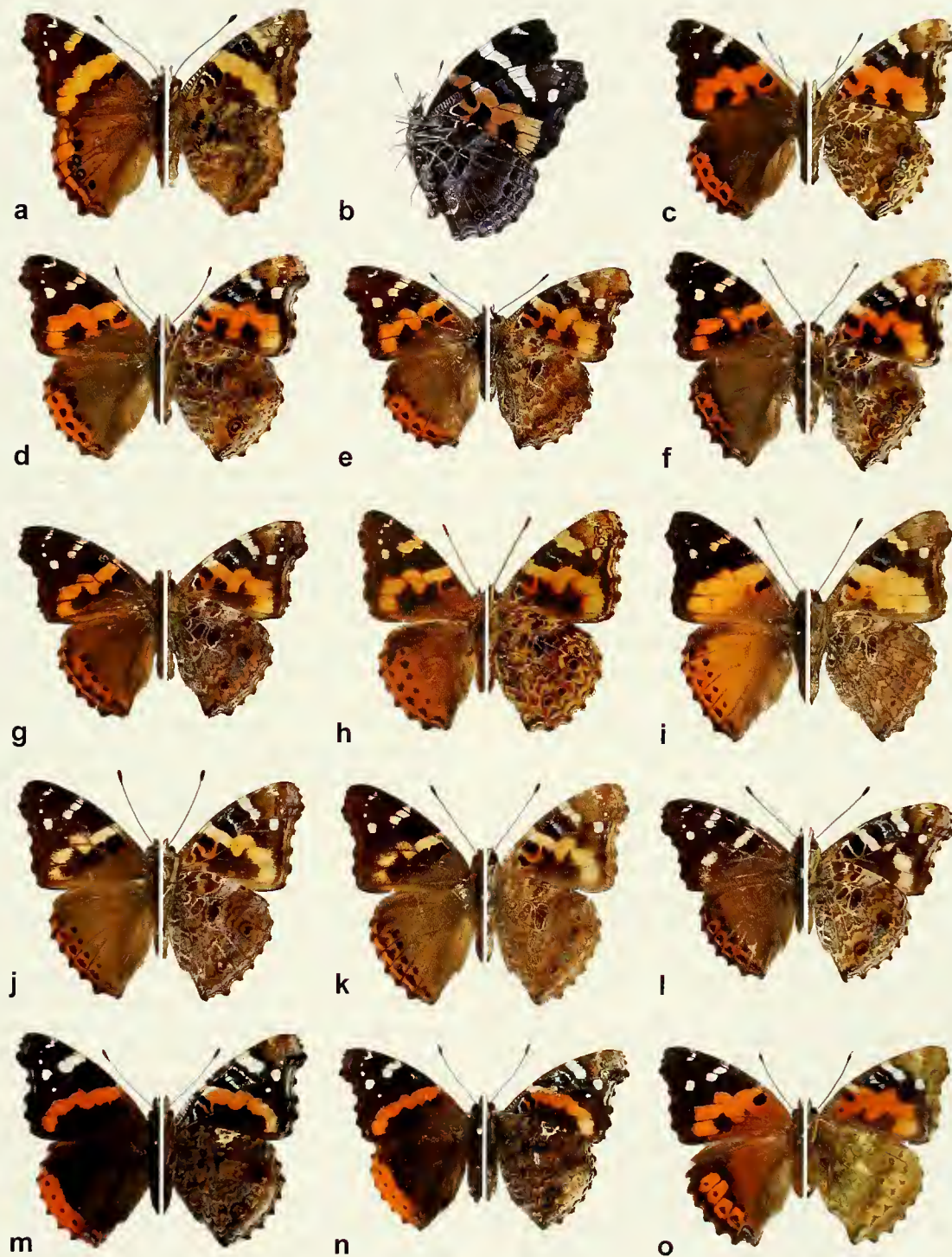


Figure 1

'ocellata'). All of this would be consistent with *V. abyssinica* being the most basal member of *Vanessa* s.s.

According to the molecular findings, within the Nymphalini, true *Antanartia* (comprising the *delius* species group of Howarth, 1966) is relatively remote from *Vanessa*. The sister group of the red admirals, including *V. abyssinica*, is shown by Wahlberg *et al.* (2005) to be the painted lady species group, and the antipodal admirals (but see also Otaki *et al.*, 2006a,b, who found less convincing evidence for these patterns of relationship). According to Wahlberg *et al.* (2005), a single remaining *Vanessa* species, the North American *V. annabella* (Field, 1971), represents a stem lineage for the whole of *Vanessa sensu lato* — suggestive of an American origin for the entire clade. This idea is strengthened by the results of Wahlberg *et al.* also showing that the entire *Vanessa* group, including *V. annabella*, has a sister-group relationship with *Hypanartia* Hübner, 1821 — an entirely tropical American genus (Willmott *et al.*, 2001). Another American butterfly that could belong to this group is *Pycina zamba* Doubleday, 1849. This relatively rare species, found from Mexico to Peru, looks reminiscent of a large *Vanessa*, feeds on Urticaceae (*Urera*), and has early stages similar to other members of the Nymphalini, including *Vanessa*, *Historis* and *Smyrna* (Muyshondt & Muyshondt, 1979; DeVries, 1987: 136).

The Species of *Vanessa sensu stricto* and their Distribution

V. abyssinica (Felder & Felder, 1867) is the smallest species in the group, comprising three races restricted to mountainous regions of East Africa (Ackery *et al.*, 1995). As foreshadowed by Nakanishi (1989) and demonstrated by Wahlberg *et al.* (2005: 238), *abyssinica* belongs to *Vanessa sensu stricto*, but this has not been signalled as a formal recombination, now done here for the sake of clarity (Appendix I).

V. atalanta (Linnaeus, 1758) is widespread throughout North America south to Guatemala, Cuba, Hispaniola, the Atlantic Islands, North Africa, and Europe through Pakistan, Kashmir and north of the Himalayas to the Amur River (Field, 1971). The American and Old World populations are divisible as separate subspecies, but are very similar.

V. tameamea Eschscholtz, 1821, the largest species of the group, is endemic to the Hawaiian Islands (Field, 1971).

V. indica (Herbst, 1794), the third species of the red admiral group as dealt with by Field (1971), and accepted by Shapiro (1992a), has since been subdivided. As currently recognized, the very widely distributed

nominotypical race is found in central and eastern Asia (Leestmans, 1978: fig. 1), occurring from northern India through Nepal and Bhutan to China, Korea, Japan, Siberia (migrants reaching the region of Lake Baikal) and far eastern Russia (migrants reaching Kamchatka: Korshunov & Gorbunov, 1995), and south to Myanmar, Thailand, Laos, Vietnam, Taiwan and northern Philippines (Luzon, Mindoro and Palawan: Treadaway, 1995: 27). The two populations named as *V. i. pholoe* (southern India) and *V. i. nubicola* (Sri Lanka) are virtually indistinguishable on the basis of their male genitalia (Leestmans, 1978) and, given their minor differences in wing pattern, this provides justification for continuing to regard these three taxa as no more than subspecies. Tsukada (1985: 303) treated the populations from southern India and Sri Lanka as the same, under the senior name *V. indica nubicola*.

V. samani (Hagen, 1895) is restricted to west Sumatra, in western Indonesia (Field, 1971).

V. dejeanii Godart, 1824 occurs as three races, one on Java, a second (very doubtfully distinct) on Bali, Lombok and Sumbawa in central Indonesia, and the third on Mindanao and Samar in the southern Philippines (Field, 1971; Treadaway, 1995). Conceivably this last taxon, *V. dejeanii mounseyi*, will prove to be a separate species.

V. buana (Fruhstorfer, 1898) is restricted to the mountains of extreme southern Sulawesi, Indonesia (Vane-Wright & de Jong, 2003). Treated by Field (1971) as one of the subspecies of *V. indica*, the male genitalia of *buana* are very distinct from those of *indica* s.s., sufficient to justify species-level status (Leestmans, 1978).

V. dilecta Hanafusa, 1992, was described as a separate species from Mt Mutis (2427 m), the highest mountain in Indonesian West Timor. The molecular results of Otaki *et al.* (2006a) suggest that this taxon is very closely related to *V. buana*, and they conclude that *dilecta* should either be treated as a subspecies of *V. buana*, or that the whole *indica* group be regarded as a superspecies. With respect to the former, the occurrence of a species on southern Sulawesi and Timor only would be a unique biogeographical pattern among the butterflies (Vane-Wright & de Jong, 2003). Our examination of the male genitalia of a specimen of *V. dilecta* (made available to us by Dr Otaki) confirms that it is almost identical to that of *V. buana*, as illustrated by Leestmans (1978: pl. 5, fig. 4). However, it also demonstrates that, as observed by Leestmans (1978) and noted by Otaki *et al.* (2006a: 365), the male genitalia of *V. nubicola*, *V. dejeanii*, *V. buana* and *V. dilecta* are all very similar, and both morphology and molecules indicate that this group forms a terminal group within

the *V. indica* complex. This clade has a distribution pattern “(2+5+6)”, which is also virtually unique: only the doubtful collective danaine taxon *Tirumala ishimoides* has a comparable range (Vane-Wright & de Jong, 2003: 219), and even this does not include Timor or Sumatra. Our knowledge of these relatively rare montane *Vanessa* taxa may still be incomplete. We suggest that, for the present at least, *V. dilecta* should continue to be regarded as a separate species.

V. vulcania Godart, 1819, is native to the Canary Islands and Madeira in the Atlantic Ocean. Treated by Field (1971) as a subspecies of *V. indica*, in his major papers addressing the question its origin, Shapiro (1990, 1992a; but see also 1992b) overlooked the important work of Leestmans (1978) demonstrating the clear separation between *V. vulcania* and *V. indica*. Despite comments to the contrary by Shapiro (1992a), *V. vulcania* is also found occasionally on the western European mainland (e.g. Opheim, 1960; Gerisch 1975, 1978; Reinhardt & Gerisch, 1982; Fernández-Vidal, 1989). However, there seems nothing to suggest that these mainland records represent anything other than occasional strays or individuals accidentally imported from the Atlantic Islands (Leestmans, 1978).

A Re-assessment of Taxonomic Affinities within *Vanessa sensu stricto*

Field (1971), Leestmans (1978) and Wahlberg *et al.* (2005; and pers. comm.) all agree that the red admirals (*Vanessa s.s.*) form a monophyletic group. However, in their independent molecular analysis, Otaki *et al.* (2006a) did not get consistent support for such a clade. Based on morphological evidence (Leestmans, 1978), *V. atalanta* + *V. tameamea* could form a sister species pair, and this has been corroborated by some molecular data (Niklas Wahlberg and Dan Rubinoﬀ, pers. comm.) although, again, Otaki *et al.* (2006a,b) report only weak support for this pairing.

According to Field (1971: 20), the five subspecies of *V. indica* that he recognized “display no differences in the male genitalia.” However, Leestmans (1978) pointed to genital characters that link *V. buana* with the other taxa found in the Malay Archipelago: *V. nubicola* (Sumatra) and *V. dejeanii* (Java to Sumbava and Mindanao) — to which assemblage the recently described *V. dilecta* (Timor) certainly belongs (Otaki *et al.*, 2006a,b; morphological evidence reported above).

As again clearly demonstrated by Leestmans (1978), although *V. vulcania* is similar to *V. indica*, it can be separated reliably on a number of small features of the male genitalia, as well as aspects of coloration. On this basis, together with its persistently red rather than more

fugitive red-orange color, Leestmans (1978) justified recognition of *V. vulcania* as another, separate species.

Niklas Wahlberg (pers. comm.) has as yet unpublished molecular data regarding interrelationships of five of the six members of the *indica* complex: *V. vulcania*, *V. indica*, *V. nubicola*, *V. buana* and *V. dejeanii* (to which *V. dilecta* must be added). The new work confirms this complex as the sister group of the *atalanta*-group. Furthermore, within the complex, *V. vulcania* appears as sister to all the Asiatic taxa. Throughout this paper we refer to (*vulcania*-group + *indica*-group) as the *V. indica* complex. Within the *indica*-group, Otaki *et al.* (2006a,b) found evidence that *dilecta* is sister to *buana*, these two together are sister to *dejeanii*, these three are sister to *samani*, and that these four altogether form a distinctive group sister to *V. indica*.

Thus the relationships of the species of *Vanessa s.s.*, based on the information outlined above, can best be summarized by the following indented table, although evidence for monophyly of the group as a whole, and the *V. atalanta* + *V. tameamea* pairing, may not be very robust:

abyssinica-group [Africa]

atalanta-group (*atalanta* + *tameamea*) [northern hemisphere]

vulcania-group (*vulcania*) [Atlantic Islands]

indica-group (*indica* (*samani*(*dejeanii* + (*buana* + *dilecta*))))
[Nepal east to Japan and south to Timor]

Possible Origins of the *V. indica* Complex in Macaronesia

As indicated, there is no record for any *indica*-like taxon in the vast area between northern India and the Canary Islands, except occasional strays in western Europe (*V. vulcania* in the Iberian Peninsula, Germany and elsewhere; remarkably, *V. indica indica* has also been recorded from central England: Bretherton, 1989). Field (1971: 24) suggested that what he treated as the disjunct Atlantic Ocean race, *V. indica vulcania*, “may have evolved from specimens accidentally introduced from India by early Portuguese traders” — but on the basis of his morphological findings, Leestmans (1978) dismissed this idea as implausible. As suggested to us by Thomas Dimock, this is also very unlikely in terms of *Vanessa* biology and its ability to remain alive on board ship for several months. Shapiro (1992a), at that point unaware of Leestmans’ work, drew attention to an earlier, alternative explanation. Kostrowicki (1969: 282) had suggested that the various

disjunct populations, notably those on the Atlantic Islands, could be relicts of a former, much wider Tertiary range. Shapiro (1992a) commented that molecular genetics could surely distinguish between two such extreme hypotheses, one requiring these Macaronesian populations of *V. indica* to be only hundreds of years old and to have gone through an initial 'bottleneck', the other implying that *V. vulcania* must be hundreds of thousands or even millions of years old. We call the first of these ideas "Field's Introduction Hypothesis" (FIH), and the second "Kostrowicki's Tertiary Relict Hypothesis (KTRH).

While KTRH appeals as a more interesting explanation, the absence of the *indica* complex anywhere in northern Europe, North Africa and North America seems surprising. However, as pointed out to us by Thomas Dimock, it would not be necessary to have continuous suitable habitat from India across the whole of Iran and Africa to Macaronesia. Indeed, large areas of unsuitable land between marginal habitats in the Mediterranean region might have made it more likely that migratory butterflies would reach distant localities, such as the Canary Islands, as they would be obliged to continue their search.

Shapiro (1992a) noted that in Macaronesia the butterfly is tied to *laurisilva* forest, considered to be a relict of former Tertiary broadleaved forests (Kostrowicki, 1969: 285; "nemoral forests": Pielou, 1979: 204–210; Miller & Miller, 1990). However, in the far east the *V. indica*-group does not seem to be confined to such habitats, ranging widely from montane areas in the tropics to a variety of cool temperate zones in the north, in the summer migrating as far as southern Siberia and Kamchatka (Korshunov & Gorbunov, 1995). If the Macaronesian populations of *V. vulcania* are genuine relicts (which must, at least, have island-hopped: Shapiro, 1992b), given the rich and varied forest habitats of North America in particular, it seems curious that no member of the *V. indica* complex has ever been found there.

If *V. vulcania* is a Relict, from Where has the *V. indica* Complex Disappeared?

As already indicated, *V. indica sensu* Field (1971) has largely been dismembered. The remaining populations now assigned to *V. indica* are divisible into just two or at most three subspecies: *V. indica indica* in the main Russian-Indo-Chinese range, including Japan, *V. i. pholoe* (Fruhstorfer, 1912) in southern India, and the very similar *V. i. nubicola* (Fruhstorfer, 1898) in Sri Lanka. As noted above, *V. vulcania* and *V. buana* were separated by Leestmans (1978) as distinct species.

These taxonomic changes were made on the basis of small differences in wing patterns and male genitalia. If correct, they offer support for KTRH rather than FIH, insofar as we generally think of species evolving over many thousands if not millions of years, rather than a few hundred generations as implied by FIH. For example, based on extensive allozyme data, Shapiro & Geiger (1989) calculated that the very similar-looking *Vanessa annabella* (North America south to Guatemala) and *V. carye* (Hübner, 1812; South America) diverged about 3 million years ago.

While according to FIH the 7000 km gap from the Atlantic islands to NE India requires no other explanation, KTRH raises the question from where else have populations of the *Vanessa indica* complex disappeared? Given the known distribution of *V. indica sensu lato*, there is little reason to suppose that the *indica* complex ever occurred in South America. On the other hand, it might seem self-evident that it must have been lost from the whole region extending from the Mediterranean to northern India, including the Alps, Balkans, Turkey, Iraq, Iran and Afghanistan (notwithstanding Dimock's suggestion above regarding migration between marginal habitat patches). However, many biotopes in these areas appear suitable for the butterflies. If so, why would they have died out in this region?

Leestmans (1978) made the interesting suggestion that during glacial maxima the *V. indica* complex could have been represented throughout what is now the so-called eremic zone, the vast region of deserts and semi-deserts that runs across almost the whole of North Africa east to Somalia and the Arabian Peninsula, and from there to the Iran Plateau, Thar Desert and Tien Shan (Leestmans, 1978: fig. 1). From southern Morocco it would have been easy for a red admiral to reach both the Canaries and Madeira. With a return to interglacial conditions, the *indica* complex populations would have died out across this huge tract as it became desertified. In contrast, the *laurisilva* forests survived on the well-watered Atlantic islands, until largely destroyed by human activity in the past few hundred years.

A possible objection to such a scheme is that, as the ice retreated northwards, what would prevent the butterflies entering the Mediterranean region? Kostrowicki (1969: 280) discussed the idea that North African mountains played an important role as refugia for butterflies, noting in particular that a number of "typical African subspecies penetrated the Iberian Peninsula." Retreating higher and higher into the mountains, perhaps the *Vanessa* populations became trapped and died out *in situ*, unable to escape northwards. However, if we set this doubt aside, under

Leestman's scenario we might expect that *V. vulcania* and *V. indica indica* would prove to be sister taxa. Leestmans further suggested that the time since *V. vulcania* became separated from the main range of what is now *V. indica* would be about 1 million years. This variant of KTRH we can call "Leestmans' Eremic Zone Hypothesis" (LEZH). A similar scenario is also entertained by Pittaway (1993: 35–36) in an effort to understand the distribution of western Palaearctic hawkmoths, and he notes *inter alia* that "by the end of the Tertiary ... most eastern Asiatic species [of plants] had vanished from Europe (c. 1 million years BP)."

There is, however, a major alternative possibility: a North American origin (Vane-Wright, in Shapiro, 1990: 222) and subsequent loss ("American Origin Hypothesis": AOH). Given the likelihood that the genus *Vanessa* is fundamentally American (stem group position of *V. annabella*; sister group relationship with *Hypanartia*), and given that *V. atalanta* occurs as two subspecies, one in the New World and one in the Old, we should consider the idea that *ur-indica* originated in the Nearctic. Could the *indica* complex, in the form of *V. vulcania*, have reached the Atlantic Islands from eastern North America, rather than North Africa, while the Asian *indica*-group species reached Asia from western North America via Beringia? *V. indica* actually occurs in Beringia during the summer months, reaching to more than 50°N in Kamchatka.

Under AOH, one might expect *V. vulcania* to be the (relatively ancient) sister group of a clade comprising all the eastern *indica*-group taxa, and this is supported by the most recent molecular findings, as summarized in the indented table above. As already noted, under LEZH we might expect *vulcania* and *indica indica* to be (more recent) sister taxa. Under FIH, if Portuguese traders were responsible, perhaps a Goanese population (*V. i. pholoe*) would be the most likely sister to *vulcania*, with a separation time of only a few hundred years. These alternatives are not supported by the current systematic arrangement (see table above).

While AOH would explain away the 7000 km gap between Macaronesia and India (under this scheme there is no compelling reason to suppose the *indica* complex ever occurred in this intervening region), it does so by substituting an even larger 10,000 km gap between Kamchatka and Madeira. Thus a choice between these two scenarios could be affected by any evidence of former presence of the *Vanessa indica* complex in either North America or the western Palaearctic/North Africa. Before turning to this issue, it is worth noting that there appears to be virtually no evidence of exclusive biogeographical connections between Macaronesia and the Indo-Australian region.

Increasing knowledge of the phylogenetic relationships of Macaronesian plants reveals that the great majority have their closest relatives in Europe and North Africa, although there do appear to be some links to East Africa, South Africa and, most notably in this context, the Americas (Carine *et al.*, 2004).

A Fossil Member of the *Vanessa indica* Complex

There is one known fossil clearly relevant to this debate, the early Oligocene butterfly *Vanessa amerindica* Miller & Brown, 1989. This was described from the Florissant formation of Colorado (dated at *ca* 35 million years BP), and the authors considered it to be most like *Vanessa indica* amongst the recent fauna (Miller & Brown, 1989). Taken at face value this is consistent with AOH, and could be another example of marked stasis coupled with local extinction that may be emerging as characteristic of butterfly evolution during the middle to late Tertiary (e.g. Hall *et al.*, 2004; Vane-Wright, 2004). Even so, this is not evidence enough to suggest that the modern distribution of *Vanessa* is somehow directly linked to the tectonic break up of the North Atlantic. This would only be plausible if the *V. indica* complex could be demonstrated to be at least 70 million years old (cf. Miller & Miller, 1990). Given the great rarity of butterfly fossils, the existence of *V. amerindica* dated at 35 mya is, however, both suggestive and challenging.

An 18th Century Record of an Apparently New Member of the *V. indica* Complex from North America

As indicated in the introduction, while researching a set of previously unpublished 18th century paintings of world Lepidoptera made by the British naturalists Henry Seymer (1714–1785) and Henry Seymer Jr, (1745–1800), we came across an image of what is undoubtedly a member of the *Vanessa indica* complex (Fig. 1b; Vane-Wright & Hughes, 2005: 165). The Seymers indicated that their painting was based on a specimen sent to them from Newfoundland, but gave no further details of date or collector. What credibility can be given to this seemingly very unlikely record?

Among hundreds of images of Lepidoptera made from the Americas, Europe, Africa, Asia and even Australia, the Seymers illustrated just three other species purportedly from Newfoundland. The island is an entirely plausible source for all three of them (details below). Moreover, their image of *Vanessa* (Fig. 1b) cannot be matched precisely to any of the known living taxa currently included within the *V. indica* complex (cf. Figs 1c–l). Neither can it be matched to *V. amerindica*,

as the fossil does not permit detailed evaluation based on wing patterns.

The other species the Seymers illustrated from Newfoundland were two swallowtails and a ghost moth: *Papilio brevicauda brevicauda* Saunders, 1869; *Papilio canadensis* Rothschild & Jordan, 1906; and *Sthenopsis purpurascens* (Packard, 1863) (Vane-Wright & Hughes, 2005). *P. brevicauda* is quite narrowly restricted to parts of Quebec and the Maritime provinces of eastern Canada, where it is "widespread and commonly encountered in Newfoundland" (Layberry *et al.*, 1998: 83). *P. canadensis* is well-known from almost all parts of Canada, including Newfoundland (Layberry *et al.*, 1998: 87–88).

S. purpurascens (Hepialidae) is one of four species belonging to the exclusively North American genus *Sthenopsis* Packard, 1865, known from USA and Canada (Nielsen *et al.*, 2000: 850). Newfoundland records for *Sthenopsis purpurascens* (Packard, 1863) are based on material housed in collections of the Canadian Forest Service (Corner Brook, NL; and Edmonton, Alberta), and Agriculture Canada Research Station (St. John's, NL). The identifications of this material (under the synonymous name *Sthenopsis quadriguttatus* (Grote, 1864)) were made by Canada Agriculture personnel in Ottawa (David Larson, pers. comm., September 2007; see also Bowers & Parly, 1996). Currently, this is the only *Sthenopsis* known from Newfoundland.

The dates for the four paintings on which these images appear are: *V. indica* complex ca 1773, *P. brevicauda* February 1776, *P. canadensis* 1772, and *S. purpurascens* ca 1773. The reason for uncertainty over the date for the *Vanessa* image is that the Seymer paintings were cropped at some point in the past to fit into a binding, and in some cases the dates have been cut off, in part or whole (Vane-Wright & Hughes, 2005: 53). In most cases other clues are available to give approximate dates, and we think that 1773 (not earlier than 1772, and unlikely to be later than 1776) is a good estimate for the date of the painting on which the *Vanessa* appears.

The Seymers misidentified the two swallowtails, but were aware that the other two insects represented undescribed species: the ghost moth they compared to *Hepialis humuli* (L.), and the *Vanessa* they noted as "Simillima *Atalanta* nostrae." These illustrations are probably the first known for all four taxa. However, at the same time Pieter Cramer (1775: 132, Pl. 84, figs E,F) presented images of a "vulcain" (Red Admiral) from China, under the name *Papilio atalanta*. His discussion indicates that he was aware of differences between his specimen and the familiar European insect. The paintings in Cramer clearly show true *Vanessa*

indica, and demonstrate that by the 1770s Chinese material of this species was already reaching European collectors.

The Seymers had a great deal of material from China, and therefore it is conceivable they accidentally mislabelled a Chinese specimen of *V. indica*, and then made a slightly inaccurate picture of it. While not error-free, the Seymer paintings are, in general, precise (Vane-Wright & Hughes, 2005: 268). In several ways the Seymer image fits *V. vulcania* far better than true *V. indica* (see below). So an alternative possibility might be that the Seymers obtained a specimen of *V. vulcania* from the Canaries or Madeira, and then made a slightly inaccurate picture of that. Plants used in horticulture were certainly available from the Canary Islands by the mid 18th century, and probably much earlier (e.g. the endemic *Isoplexis canariensis*, named by Linnaeus in 1753; Vane-Wright & Hughes, 2005: 212). However, *V. vulcania* was not described until 1819, and very few other endemic Atlantic island Lepidoptera were named before that time: *Pararge xiphia* (Fabricius, 1775), endemic to Madeira, is a rare example (Weingartner *et al.*, 2006). There is absolutely nothing to suggest that the Seymers ever received any insect material from the Atlantic Islands (Vane-Wright & Hughes, 2005: 254, table 1), whereas they undoubtedly did obtain a considerable number of insects from Newfoundland and China.

If we assume that all four taxa stated by the Seymers to have come from Newfoundland originated from a single source, then these specimens must have been collected before 1772. We found no further information concerning their possible origin (Vane-Wright & Hughes, 2005: 260), although we speculated that Joseph Banks might have collected this material during his visit to the island in 1766 (see Lysaght, 1971). By about 1775 the Seymers were also receiving specimens from Newfoundland collected by a Mr Top, an island resident. There is nothing to suggest that Banks visited China during this period, nor Top either.

As there is no reason to doubt the provenance of the other Lepidoptera reported by the Seymers from Newfoundland, this putative record for the *Vanessa indica* complex in Canada should be given credence. The evidence of *Papilio brevicauda* is significant, as it is a narrowly distributed species found only in north-eastern Canada. We are thus confident that the *Vanessa* image must be based on one or more specimens that came into the Seymers' possession ca 1770, and we see no particular reason to doubt the given provenance of Newfoundland, and some reasons to accept it. This includes our conviction that the image (Fig. 1b), which is detailed, cannot be matched precisely to any of the

old world taxa that make up the *V. indica*-group, including *V. indica indica*, or to *V. vulcania* (Figs 1c–l).

However, Thomas Dimock (in litt., 2007) has pointed out six peculiarities of the Seymer image which do give rise to questions regarding its accuracy—were it to be assumed that it is based on either *V. indica* or *V. vulcania* with incorrect provenance. We comment on each of these points, in turn:

1. “First is the extent and intensity of the blue markings on the HW underside, much bluer than any known *Vanessa* today.” As reproduced there is a blue cast. The original paintings are no longer readily available to us for re-examination. They were photographed as large format transparencies in 1992, scanned in 2004, and the resultant “tif” file was transformed in Adobe Photoshop to make the images presented here, in 2006. If you take a flash photograph of the underside of a *V. vulcania* specimen you will not see a blue cast, but you will see a very strong blue area at the end of the forewing discal cell, and a complete series of post-ocellar blue marks in cells R_1 – CuA_2 , as in the Seymer image.

2. “No living species of *Vanessa* has such a gigantic white costal bar extending into cell M_3 . . . when measured along its greatest length, [it] reaches 7/15 (46.7%), or nearly half of the way to the wing margin near the tornus . . . The white bar in *V. vulcania* (Fig. 1c) reaches only 4/15 (26.7%), of the distance to the tornus.” Using the large white submarginal spot in cell M_2 as a marker, we suggest that the Seymer image does not show this bar extending into cell M_3 , but crossing cell M_2 to end at vein M_3 . Measured on a full-size photograph of the Seymer image, we make the extent 42.5%, not 46.7%. The extent of this mark in *V. indica* and *V. vulcania* can often exceed 30%, but undoubtedly this does represent a major difference to these species. Is such an extent impossible? Frohawk (1938: plate 20, p. 86) illustrates an aberration (‘albo-punctura’) of *V. atalanta* from Erith, England (now preserved in the BMNH), in which the outer half of forewing cells M_2 and M_3 are largely filled with white. In cell M_2 it appears to consist of an extension of the white bar that has fused with the main submarginal white spot. Measuring on the underside from the costa, where the bar elements commence, to the margin of white area at vein M_3 , gives a value of 41% for the ratio in this *atalanta*. Making these measurements to vein M_3 in *V. vulcania* and *V. indica* typically gives 38–40%. In subgenus *Cynthia* the white bar often extends back to vein M_3 . Field (1971: fig. 158) illustrates a specimen of *V. (C.) annabella* in which this is so; it has a value of 38.5%. We conclude that the Seymer figure is not so extreme as Dimock suggests, and is not implausible.

3. “No living species has the small posterior extension of this bar extending from the distal side of the bar, as the painting has.” It is certainly true that in the great majority of *Vanessa* (*Vanessa*) specimens that have this small extension (not all do), it arises from the proximal side of the bar. However, in such cases this extension occurs in the anterior half of cell M_2 , whereas the Seymer image shows this area filled with white and contiguous with the element of the bar in cell M_1 . The extension in the Seymer image occurs in the posterior half of cell M_2 , reaching vein M_3 as already discussed. So in this case we are not comparing like with like. We have searched for *Vanessa* (*Vanessa*) with the posterior half of cell M_2 filled with white but, apart from the Frohawk example described above, which is too extreme, we have not found anything really comparable. However, in *Vanessa* (*Cynthia*), the bar often crosses the whole of M_2 , and where it does so, the extension into the posterior half of the cell can be distal. Field (1971: figs 133,134) illustrates a specimen on *V. (C.) terpsichore* in which the configuration of the whole bar approaches that of the Seymer image. We conclude that if the Seymer image does represent a *Vanessa* in which the bar reaches across the whole of cell M_2 , the distal extension is entirely plausible.

4. “In the painting, the hindwing ocelli are all longitudinally flattened, equal in size, and the anterior four are in a very straight line, unlike all other *Vanessa*.” We agree that this configuration looks odd. The most complete ocellus on the hindwing underside in most *V. indica* and *V. vulcania* is the most posterior one, in cell CuA_1 , and the Seymer image conforms in this regard. In *V. indica* and *V. vulcania*, however, as in other *Vanessa*, the more anterior border ocelli vary in size and shape, but have their centers located on a smooth arc, parallel to the curve of the wing margin.

5. “The painting shows a total of six ocelli or ocelli without pupils. *Vanessa* have only five, never a sixth ocellus in cell $Sc + R_1$.” We also agree that all *Vanessa* we have examined have only five border ocelli on the hindwing, occurring in cells R_5 to CuA_1 inclusive. We have not seen any *Vanessa* with a clear ocellus in cell R_1 , although this is part of the nymphalid groundplan, and can be seen very clearly in some species (e.g. *Charaxes analava*: Nijhout & Wray, 1986). According to Beldade & Brakefield (2003: 176), all marginal wing cells appear to have the potential to produce eyespots, and laboratory selection experiments rapidly reveal the capacity of species to produce ocelli in cells that do not normally exhibit them. “Eyespot number is not a very fixed trait even within a species” (Antónia Monteiro, in litt., July 2007). In conclusion on this point, we agree that the configuration of the hindwing ocelli in the

Seymer image are uncharacteristic of known *Vanessa* species, and could either reflect the fact that, as we suggest, this is a new species, or that the Seymer image is inaccurate in this respect. The hindwing underside pattern of *Vanessa* is very complex, and is a considerable challenge for any artist. Another possibility is that the Seymers' specimen had the apex of the hindwing missing, and Henry Jr. simply interpolated what he thought it should look like. There is ample evidence that the Seymers 'perfected' incomplete specimens based on their general knowledge of similar species.

6. "Finally, look at the hindwing on the painting and notice how far distally from the dark discal spot that vein M_3 branches from Cu_1 . It should arise from the posterior end of the discal spot, not 3mm distally. Differences this great have been used to distinguish genera." There seems no doubt that the hindwing venation has been misinterpreted in the Seymer image—and the forewing venation is also incorrect. Very few illustrators at this date produced accurate images of Lepidoptera wing venation. It was not until William Jones (1794) published his ground-breaking comparative work, some 20 years later, that lepidopterists regularly started to render accurate wing-vein schemes.

In conclusion, Dimock comments "Of course, all of these "inaccuracies" support the authors' the hypothesis [see below] that the painting is of an extinct species." With respect to points 1–6 raised by Dimock above, on reflection we consider that 1–3 are consistent with our view that the Seymer image does represent an extinct species, while 4–6 probably do reflect genuine inaccuracies.

Shapiro says that *V. vulcania* is more like far-eastern *V. indica* than SE Asian, and that it also varies in the direction of Holarctic *atalanta*. However, as pointed out by Bascombe *et al.* (1999), *V. indica indica* is a migrant, and it hardly varies over its extensive range. John Tennent (2005, and pers. comm.) has related how he remembers "seeing *indica* occasionally in Hong Kong ... it's a small pale shadow of the brilliant, whopping thing that occurs on Madeira and the Canaries." The Seymer paintings were executed life size (Vane-Wright & Hughes, 2005), and the forewing length of the supposed Newfoundland specimen, as figured, measures 35 mm — quite large for any red admiral except *V. tameamea*. While examination of a long series of *V. indica* from China and a considerable number of *V. vulcania* in the Rothschild Collection (at the Natural History Museum, London) confirms that the latter is undoubtedly "redder" in some sense than the more orange eastern taxon, any impression of larger size must be an illusion or a sampling artefact. A few female

specimens from China equal or slightly exceed a forewing length of 35 mm, which is also about the maximum found among material from the Canaries. In this context it is notable that the forewing lengths of the two original specimens of *V. amerindica* are given as 24 mm and 27 mm (Miller & Brown, 1989: 1). Some individuals of both *V. indica* and *V. vulcania* have a forewing length as short as 25 mm, or even less.

The persistent red coloration of *V. vulcania* appears to be a specific feature (fresh *V. indica* may be almost as red, but invariably fade to orange during life, or post-mortem). From this it would seem that, on the basis of its more orange color, Seymer's image (Fig. 1b) does not represent *V. vulcania* (Fig. 3), but this cannot be given much weight. Assuming the postdiscal white patterning of the forewing has been rendered accurately (see discussion if Dimock's points 2 and 3, above), it is not *V. indica* either (Figs 1d–f). As Higgins & Riley (1980: 102) point out, in the Canary Red Admiral "the short band of three white spots runs from the costa at a right angle", whereas in *V. indica* this band is oblique. This reliable difference is most readily appreciated by extending an imaginary line along the distal margin of this short band. In *V. indica* this imaginary line will always enter (at the very least touch) the large white submarginal spot in cell M_2 , whereas in *V. vulcania* such a line is always proximal to the smaller M_2 white spot, and never runs through it.

As examination of Field (1971: figs 33–80), Tsukada (1985: plate 49) and Figs 1a–o will confirm, the condition of this character in *V. indica* is shared with all other known *Vanessa* s.s., including *V. abyssinica* — *V. vulcania* being the only exception. This feature thus represents an apomorphy for the *V. vulcania*-group, and on this basis we suggest that the Seymer image, which shows exactly the same configuration (despite the very large submarginal spot shown in cell M_2), represents an undescribed and recently extinct member of the *V. vulcania* species group from North America. This previously unknown species differs from *V. vulcania* in having the principal forewing band orange rather than bright red; in having the short precapical forewing band composed of four elements (in cells C, R, M_1 and M_2) in which the white element in the anterior half of M_2 is the same width as in M_1 , with a small distal extension into the posterior half of M_2 , instead of small proximal extension to the white mark in M_1 that is confined to the anterior half of M_2 ; and in having the submarginal white spot in forewing cell M_2 large (ca 2 mm diameter), not small as in *V. vulcania* (usually about 1 mm diameter, although it can be larger).

Finally, regarding the plausibility of this apparent record, it is necessary to consider environmental

conditions in Newfoundland. Being unable to survive harsh winters, *Vanessa* species only occur in far northern areas, such as Lake Baikal (*V. indica*) and Newfoundland (*V. atalanta*), by annual remigration from the south. If, as pointed out to us by as Thomas Dimock, we accept the Seymer record as genuine, then his material must have been collected in the summer or autumn months, and been derived, directly or indirectly, from spring or early summer migrants from the far south. In which case one would expect that early collectors would have obtained this species from source colonies in the USA — as in the case of *Vanessa (Cynthia) virginensis* (Drury, 1773), first discovered in the USA, and which only reaches Newfoundland during the summer months (Layberry *et al.*, 1998). If it is assumed that such a butterfly would have been common and abundant, like most familiar *Vanessa* species, then this is puzzling and must add to the uncertainties regarding the Seymer record. On the other hand, most genera do include genuinely rare species, often including some that appear close to extinction.

Given the various doubts indicated above, and that this insect is known only from a painting which could be inaccurate in details of pattern and provenance, we do not propose to give it a formal name. However, should the existence of such a *Vanessa* in North America ever be independently confirmed, we urge that it be named in honor of Henry Seymer.

CONCLUSIONS

While Wahlberg *et al.* (2005) conclude that the Palaearctic region and subsequent dispersal played a crucial role in the diversification of the *Nymphalis*-group *sensu lato*, we suggest here that North America could have been the origin for *Vanessa*, including not only the painted ladies, but also the red admirals. Were this to be the case, it would be plausible that offshoots of the group reached the Old World on several occasions, giving rise to *V. abyssinica* in Africa, *V. atalanta atalanta* in the Palaearctic, *V. tameamea* in the Pacific, and *V. vulcania* in the Atlantic. Under this model the *V. indica*-group was established from the same American stem-lineage as *V. vulcania*, reaching Asia via Beringia or the Pacific rather than across the Atlantic and through the Mediterranean and North Africa.

If the *indica* complex did evolve in North America 35 million or more years ago (Miller & Miller, 1990), then the distance over which the postulated Atlantic colonisation event took place would have been less than current geography implies. According to the reconstructions of Owen (1983: e.g. map 22), at 180–200 mya, the crust that is now Newfoundland held

a position relative to north-western Africa more or less identical to where Madeira lies today. While this neat correspondence makes the point, it is undoubtedly misleading. Moreover, the Atlantic islands are oceanic, and have never been connected to any mainland area. According to current estimates, Madeira is little more than 5 million years old, although the origin of nearby Santo Porto may be as old as 14 mya, and the oldest island in the Canaries (Fuerteventura) probably exceeds 20 my (Hughes & Malmqvist, 2005: 292). The presence of the endemic *Vanessa tameamea* on Hawaii surely gives convincing evidence of the ability of the red admirals to colonize remote oceanic islands. *V. indica* and *V. atalanta* readily travel long distances and, as their annual re-colonisation of boreal areas each spring demonstrates, they can occur in almost any suitable habitat if weather conditions permit.

In final conclusion, we suggest that, even as recently as 1770, an extinct member of the *Vanessa indica* complex may have occurred in North America, and was able to reach Newfoundland during summer months. While not substantiated, this suggestion cannot be discounted on the basis of the extant distribution of the *V. indica* complex. Molecular investigations already appear decisive regarding rejection of an introduction hypothesis (FIH) in favor of some form of tertiary relict hypothesis (KTRH) for the existence of the Atlantic Islands endemic, *V. vulcania*. Molecular systematics could also be used to evaluate the plausibility of the former occurrence of the *indica* complex in North America, based on the different phylogenetic implications of extinction in Old World eremic zone, coupled with divergence about one million years ago (LEZH, with *V. vulcania* and *V. indica indica* as putative sisters), vs. extinction in North America, coupled with divergence several millions of years ago (AOH, with *V. vulcania* and the whole Asiatic *indica*-group as putative sisters). Current evidence already favors the latter interpretation. We urge molecular systematists to try to obtain multiple samples of all *Vanessa* taxa (subspecies as well as species) and, by using data from numerous genes, attempt to give a truly robust answer to what remains a fascinating biogeographical question: how did this most peculiar distribution come about?

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APPENDIX I

Checklist of the nine extant species of the subgenus *Vanessa* (*Vanessa*) currently recognized, and their accepted subspecies. *Pyrameis abyssinica* Felder & Felder, 1867, is here formally transferred to *Vanessa*, based on the results of Nakanishi (1989) and Wahlberg *et al.* (2005), and the discussion presented above. In addition, we include the fossil taxon *V. amerindica* Miller & Brown, and note the unnamed *indica*-complex taxon reported ca 1773 by Henry Seymer and Henry Seymer Jr. (see text). Among recently described *Vanessa* taxa, *V. pulchra* Chou, Yuan, Yin, Zhang & Chen, 2002, appears to be an aberration of *V. (Cynthia) cardui* (L.), and is not included here.

VANESSA (VANESSA) Fabricius, 1807 (type species: *Papilio atalanta* Linnaeus, 1758)
(Lepidoptera: Papilionoidea: Nymphalidae: Nymphalinae: Nymphalini: Nymphalina)

†*V. (Vanessa) amerindica* Miller & Brown, 1989 [USA (Florissant formation, Colorado; Oligocene fossil)], incertae sedis

†*V. (Vanessa)* sp. nov. [North America, Newfoundland, circa 1770; apparently extinct; see text], *vulcania*-group

1 *V. (Vanessa) abyssinica* (Felder & Felder, 1867), **comb. nov.**

abyssinica abyssinica (Felder & Felder, 1867) [Ethiopia]

abyssinica jacksoni (Howarth, 1966) [Kenya, northern Tanzania], **comb. nov.**

abyssinica vansomeri (Howarth, 1966) [western Uganda, Rwanda, Democratic Republic of the Congo (Kivu, Ituri)], **comb. nov.**

2 *V. (Vanessa) vulcania* Godart, 1819 [Spain (Canary Islands), Portugal (Madeira), occasional records from mainland of western Europe] [Higgins & Riley, 1980, considered *vulcania* to be a synonym of *V. calliroe* (Hübner, 1808); we follow Aguiar & Karsholt, 2006, in continuing to employ Godart's name]

3 *V. (Vanessa) indica* (Herbst, 1794)

indica indica (Herbst, 1794) [northern India, Nepal, Myanmar, Thailand, Laos, Cambodia, Vietnam, China, Korea, Russia (Siberia, Kamchatka, Sakhalin), Japan (including Ryukyu Islands), Taiwan, Philippines (Luzon, Mindoro, Palawan)]

indica pholoe (Fruhstorfer, 1912) [southern India (western Ghats)]

indica nubicola (Fruhstorfer, 1898) [Sri Lanka]

4 *V. (Vanessa) samani* (Hagen, 1895) [Indonesia (Sumatra)]

5 *V. (Vanessa) dejeanii* Godart, 1824

dejeanii dejeanii Godart, 1824 [Indonesia (Java)]

dejeanii sambaluna (Fruhstorfer, 1898) [Indonesia (Bali, Lombok, Sumbawa)] [synonymized with *dejeanii dejeanii* by Field, 1971, but maintained as distinct by Tsukada, 1985]

dejeanii mounseyi (Talbot, 1936) [Philippines (Mindanao, Samar)] [possibly a distinct species]

6 *V. (Vanessa) buana* Fruhstorfer, 1898 [Indonesia (southern Sulawesi)]

7 *V. (Vanessa) dilecta* Hanafusa, 1992 [Timor] [Otake *et al.*, 2006a, suggest that this may be a subspecies of *buana*, but provisionally maintained here as a full species—see text]

8 *V. (Vanessa) atalanta* (Linnaeus, 1758)

atalanta atalanta (Linnaeus, 1758) [Atlantic islands, North Africa (south to northern Chad), Europe and temperate Eurasia eastwards to Pakistan, Kashmir, northern Himalayas and the Amur River]

atalanta rubria (Fruhstorfer, 1909) [Canada, USA, Mexico, Guatemala, Cuba, Haiti, Dominican Republic]

9 *V. (Vanessa) tameamea* Eschscholtz, 1821 [USA (Hawaii)]